VEGETATION STRUCTURE AND THE INTERCEPTION OF ACIDIC DEPOSITION BY OMBROTROPHIC MIRES

J.A. LEE and S.J. WOODIN
Department of Environmental Biology, The University, Manchester M13 9PL, UK

Abstract

Ombrotrophic mires are usually dominated by *Sphagnum* species which form an almost continuous carpet largely intercepting the atmospheric supply of elements in wet and dry deposition. In unpolluted conditions, some essential elements, *e.g.*, nitrogen, are immobilized by these bryophytes and do not reach the roots of higher plants in appreciable quantities. Under these conditions, *Sphagnum* species can be shown to be closely coupled to the atmospheric nitrogen supply, inducing nitrate reductase activity in response to nitrate ions in each wet deposition event. In conditions of high acidic deposition this coupling breaks down, and nitrate supply is in excess of nitrate utilization, leading to nitrate appearing in *Sphagnum* throughfall and entering the rooting zones of the higher plants. The importance of *Sphagnum* species as interceptors of wet, dry and occult deposition is examined, and the ecological importance of a breakdown in the vegetation structure of mires as the result of acidic deposition is discussed.

Introduction

Ombrotrophic mires show marked stratification, and are almost unique amongst ecosystems in that many bogs are dominated by bryophytes. Mosses of the genus *Sphagnum* form an almost continuous carpet over the surface of the mires with different species inhabiting pools, lawns and hummocks. The hummocks may also support extensive mats of another bryophyte, *Racomitrium lanuginosum* (Ehrh. ap. Hedw.) Brid., a moss which itself may achieve dominance in heaths on rock detritus on exposed summits. Through these moss carpets appear the shoots of higher plants, notably members of the Cyperaceae and dwarf shrubs of the Ericaceae. A superficial examination of the bog surface may suggest that these higher plants are in fact the dominants, but in ombrotrophic mires at least this can readily be shown to be a misconception. The vegetation is insulated from the underlying mineral soil or groundwater by an accumulation of peat which is commonly from 0.5–5.0 m in depth. In many of these mires, the vegetation and the surface peat (the acrotelm) lies on top of a virtually impervious deeper and anaerobic peat layer (catotelm). Although the roots of some plants do penetrate the catotelm, the source of elements for the growth of most higher plants comes from the partial decomposition of the vegetation forming the peat in the acrotelm or from the atmosphere, the latter providing the only primary source of elements to replenish those not released by decomposition. The higher plants may initially intercept some of the atmospheric supply on their shoots, but it is probable that only a very small proportion of this will penetrate through the cuticles directly into the shoot cells, and that precipitation will eventually bring almost all of the

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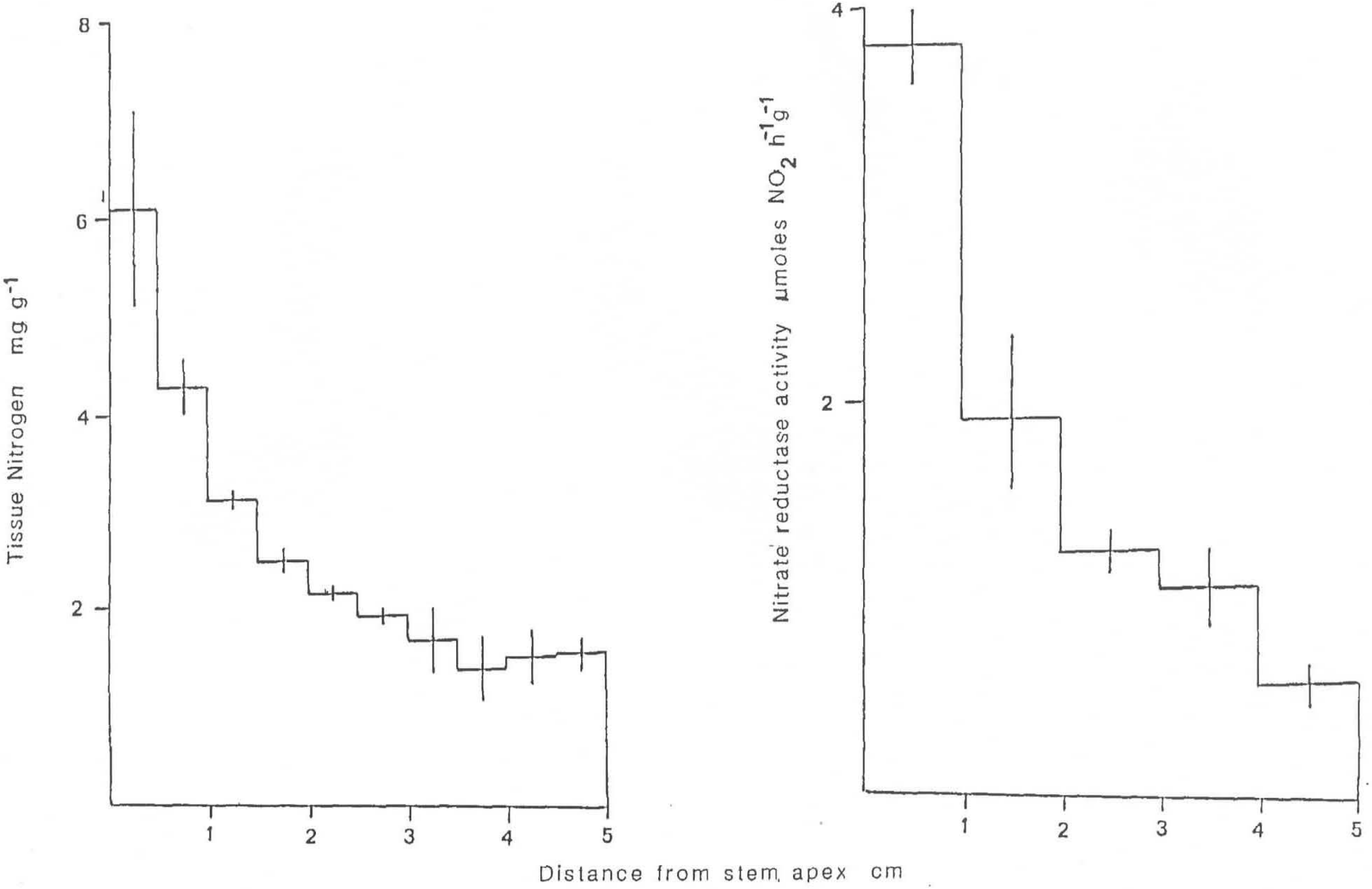

Fig. 1. Nitrogen concentration (mg g^{-1} dry wt.) and nitrate reductase activity (μmol $NO_2^- h^{-1} g^{-1}$ dry wt.) in *Sphagnum capillifolium* with distance from the stem apex (cm). Vertical bars are ± 1 S.E., $n = 4$.

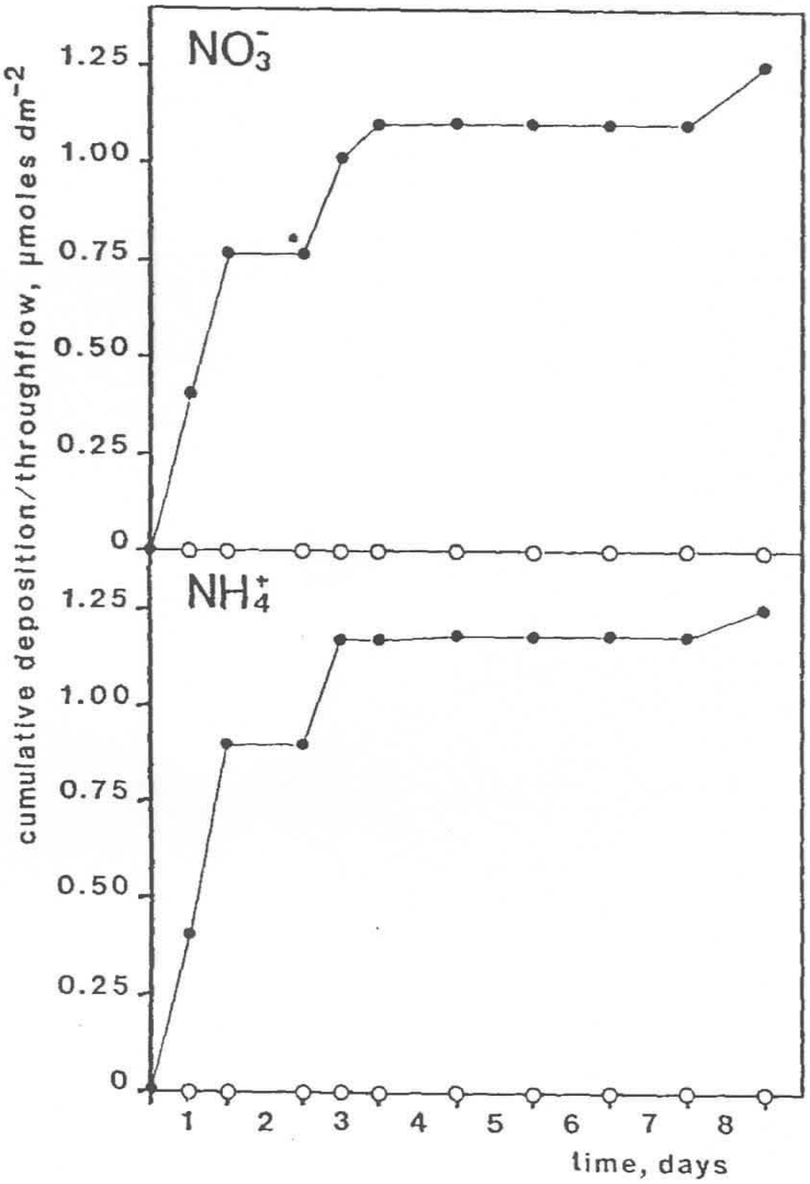

Fig. 2. Cumulative nitrate and ammonium (µmol dm^{-2}) deposited to (●) and passing through (○) mats of *Sphagnum capillifolium* in northern Sweden. Data from Woodin and Lee (1987a).

atmospheric element supply to the surface of bryophyte carpet by throughfall or stemflow.

Vegetation structure and atmospheric element interception

The bryophytes lack cuticles, and with leaves one cell thick, are readily positioned to capture and to utilize the atmospheric supply, and thus to determine the proportion of it immediately available to the roots of higher plants. An examination of the stems of *Sphagnum* species reveals that the greatest physiological activity and the contents of some important growth-limiting elements, *e.g.*, nitrogen, are concentrated in the apical region (Fig. 1). The fall in activity and tissue element concentration with distance from the apex is usually rapid, and this suggests that only a small proportion of the primary source of these elements penetrates directly even to the surface roots of the higher plants, particularly if these

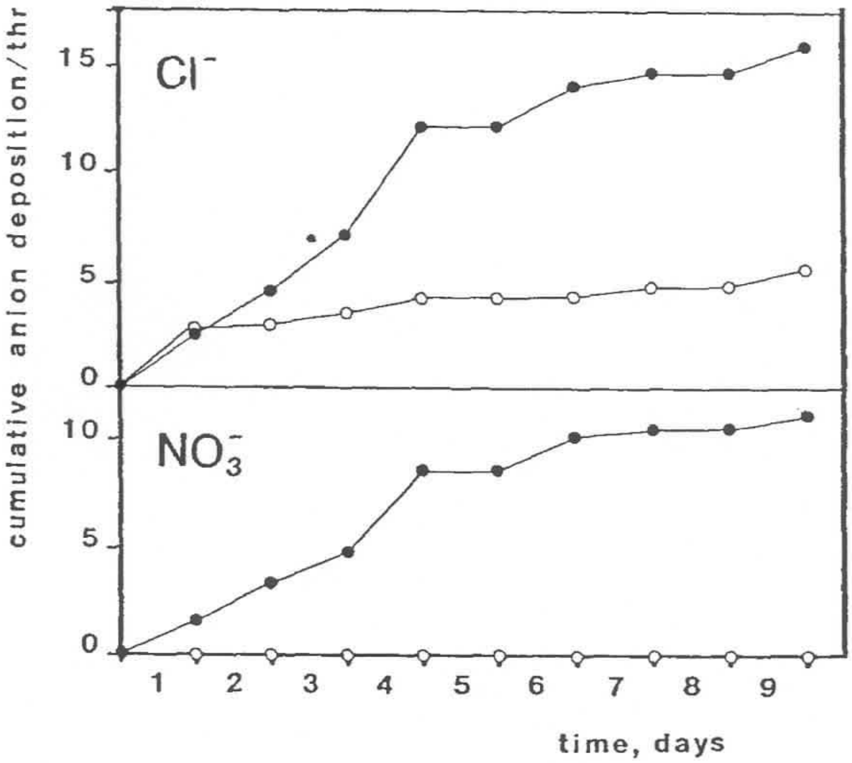

Fig. 3. Cumulative chloride and nitrate (μmol dm^{-2}) deposited to (●) and passing through (○) mats of *Sphagnum capillifolium* in northern England. Data from Woodin and Lee (1987a).

elements are required in large amounts by the moss species relative to the supply. The deeper roots, often concentrated in the region of non-green and decaying bryophyte stems, are probably dependent predominantly on element re-cycling as the source of mineral nutrients. An example of the partitioning of ions from the atmosphere in a subarctic ombrotrophic mire is shown in Fig. 2. Cores of *Sphagnum fuscum* (Schimp.) Klinggr. were cut from a mire surface and were trimmed to 4.5 cm in length. The cores were placed at natural shoot densities in small lysimeters and were inserted in the mire such that the surface of the moss was flush with the undisturbed *Sphagnum* carpet (for further details see Woodin and Lee 1987a). Bulk deposition of nitrate and ammonium ions to the mire surface was also measured. Figure 2 shows that over an eight-day period, throughflow contained no measurable nitrate and ammonium ions, although these ions were readily detectable in the bulk deposition. Thus the apical portions of *Sphagnum fuscum* stems were able to immobilize the atmospheric combined nitrogen deposition, supporting the conclusions of Rosswall and Granhall (1980) from another subarctic mire that the bryophytes effectively monopolize the atmospheric supply of this element. The degree to which this immobilization occurs will depend upon the growth demands of the *Sphagnum* for the element in question and its atmospheric supply. Figure 3 compares the immobilization of chloride and nitrate ions by *Sphagnum capillifolium* (Ehrh.) Hedw. in a similar field experiment to that described above. The chloride, with a higher total deposition over the period, and with a much lower requirement by the plant for growth, was not completely immobilized. Approximately one third of the apparent atmospheric supply passed through the living *Sphagnum* carpet and would presumably have been available to the roots of higher plants. Under natural conditions, immobilization of the atmospheric nitrogen supply (Figs 2 and 3) is probably a principal role of the *Sphagnum* carpet, and may be an important determinant of the dominance of these species since it effectively reduces the nitrogen supply to the higher plants making them almost entirely dependent on the slow mineralization of the element from dead *Sphagnum* stems. In relatively unpolluted regions of Britain concentrations of approximately 20 μM nitrate and ammonium in precipitation are typical now (Barrett *et al.* 1983), but mean annual concentrations of nitrate at least may have increased three to four times in the last century (Lee *et al.* 1987), and data from the Greenland ice-cap suggests that at even very remote sites nitrate concentrations in snow may have doubled since 1890 and sulphate concentrations have trebled (Delmas 1986). Concentrations of nitrate and ammonium ions in snow at the remote arctic sites are still rather less than 1 μM, which suggests, together with the information above, that *Sphagnum* species are adapted to utilize extremely low concentrations of these ions, effectively scavenging them, in the case of blanket mires at least, from a large volume of precipitation and effectively denying this source of combined nitrogen to the higher plants. Rates of nitrogen fixation in these mires are usually low (see *e.g.*, Rosswall and Granhall 1980) and the rate at which this source of nitrogen becomes available to higher plants or *Sphagnum* species is very uncertain.

Physiological responses to nitrate deposition in *Sphagnum*

Further evidence of the close coupling of ombrotrophic *Sphagnum* species to the atmospheric nitrogen supply can be sought through studies of nitrate assimilation. The first, and rate limiting, enzyme of nitrate assimilation, nitrate reductase, is substrate inducible, a property which can be used to examine plant responses to atmospheric deposition. Within limits the activity of this enzyme in *Sphagnum* is proportional to the $\log_e$ nitrate concentration in precipitation under field conditions (Woodin and Lee 1987b). Observations on the response of *Sphagnum* species to 'natural' rain events were made at Abisko, northern Sweden, a site remote from urban and industrial influences, where atmospheric pollution may have had relatively little influence on the vegetation (see Malmer and Nihlgård 1980). Figure 4 shows the nitrate reductase activity of *Sphagnum fuscum* in relation to nitrate deposition in bulk precipitation at an ombrotrophic mire site during the summer of 1985. Each precipitation event resulted in the rapid induction of the enzyme, the activity declining following the end of the event as the nitrate was depleted. Woodin *et al.* (1985) showed a similar response to deposition events in the summers of 1983 and 1984 at this site, and it can be assumed that the 'natural' utilization of nitrate by the moss involves the repeated induction of nitrate reductase activity. Thus not only is the nitrate absorbed by the *Sphagnum* plants, it is probably rapidly utilized.

Responses to polluted environments

The repeated induction of nitrate reductase activity in *Sphagnum* by 'unpolluted' precipitation events is a function of the nitrogen requirement of the moss and the

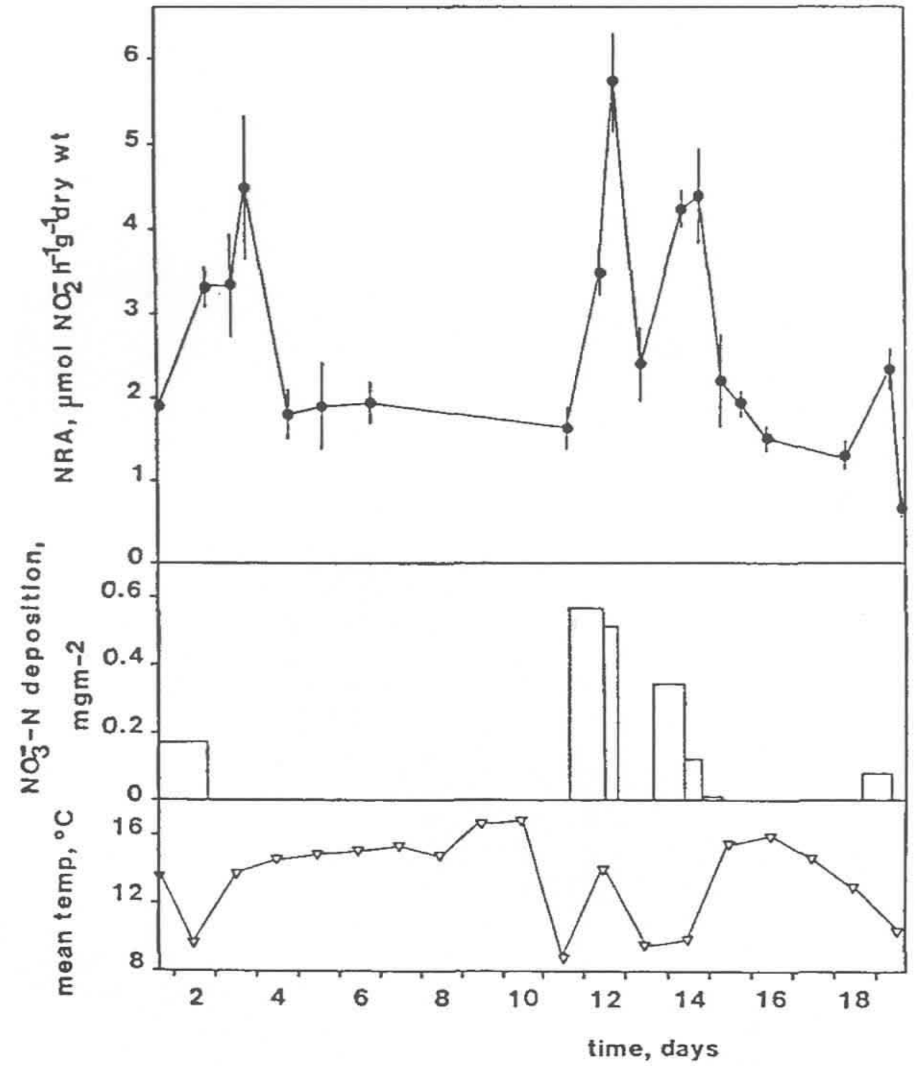

Fig. 4. Nitrate reductase activity in *Sphagnum fuscum* (μmol NO_2^- $h^{-1}g^{-1}$ dry wt.) (●) in relation to NO_3^- –N deposited (mg m^{-2} in northern Sweden, July 1985. (▿) Mean air temperature at the site. Vertical bars represent ± 1 S.E., n = 4.

rate of supply of the element. Artificially increasing the rate of nitrate supply at a mire site in northern Sweden by the addition of 'rain events' containing 1 mM nitrate reduced the cumulative induced nitrate reductase activity at each successive rain event (Woodin *et al.* 1985). This was most probably the result of the accumulation of a soluble nitrogen compound (possibly glutamine) in the cells of the moss causing inhibition of enzyme synthesis, and represents a mechanism to limit the assimilation of inorganic nitrogen when the supply exceeds the growth or storage demand. It could be predicted therefore that the transfer of moss from an 'unpolluted' environment to a polluted one would lead to a similar uncoupling of nitrate assimilation from nitrate deposition. Figure 5 shows the nitrate reductase activity of plants from an indigenous population of *Sphagnum cuspidatum* Ehr. ex Hoffm. at a polluted site in the southern Pennines of England, approximately 20 km downwind of a major conurbation (3 million inhabitants), and compares it with that of plants transplanted to the polluted mire from a relatively unpolluted North Wales population, approximately 120 km upwind of the conurbation. The 'unpolluted' North Wales plants showed a rapid induction of nitrate reductase activity to the first and largest nitrate deposition event, only a small

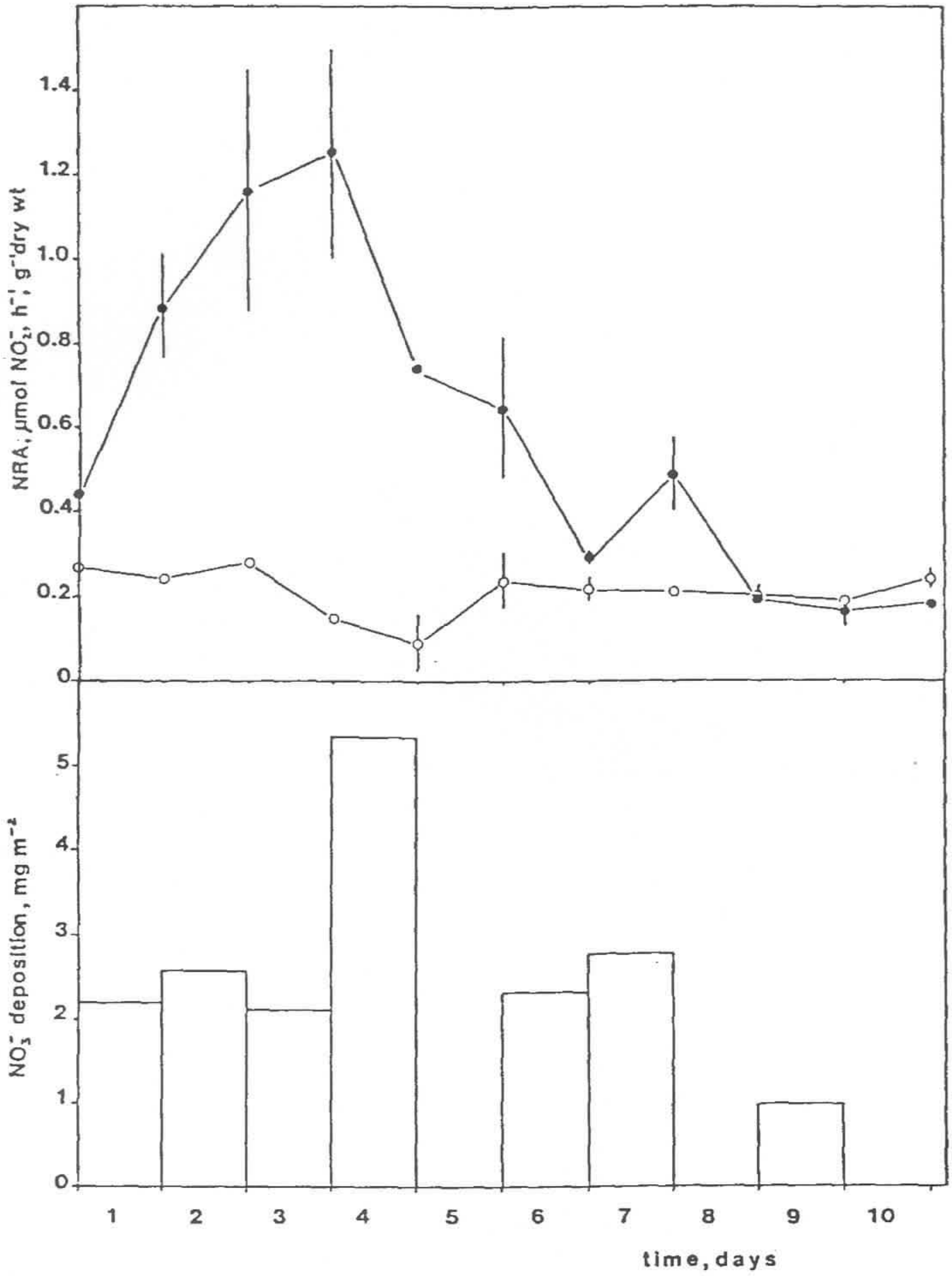

Fig. 5. Nitrate reductase activity in *Sphagnum cuspidatum* (μmol $NO_2^- h^{-1} g^{-1}$ dry wt.) from North Wales (●) and the southern Pennines (○) in artificial pools in the southern Pennines, in relation to NO_3^-–N deposition. Data from Lee *et al.* (1987).

response to the second, and none to the third and smallest one. The indigenous population showed no induction of nitrate reductase activity by these deposition events, and laboratory experiments also show no inducibility of the enzyme in plants of this population immediately after collection from the field. The southern Pennine plants have very high tissue nitrogen concentrations (usually > 20 mg g^{-1} dry weight of N) compared to plants from the 'unpolluted' site (c. 13 mg g^{-1} N), and this lack of nitrate reductase induction by the atmospheric supply suggests that the plants have a supra-optimal nitrogen content, the lack of induction being

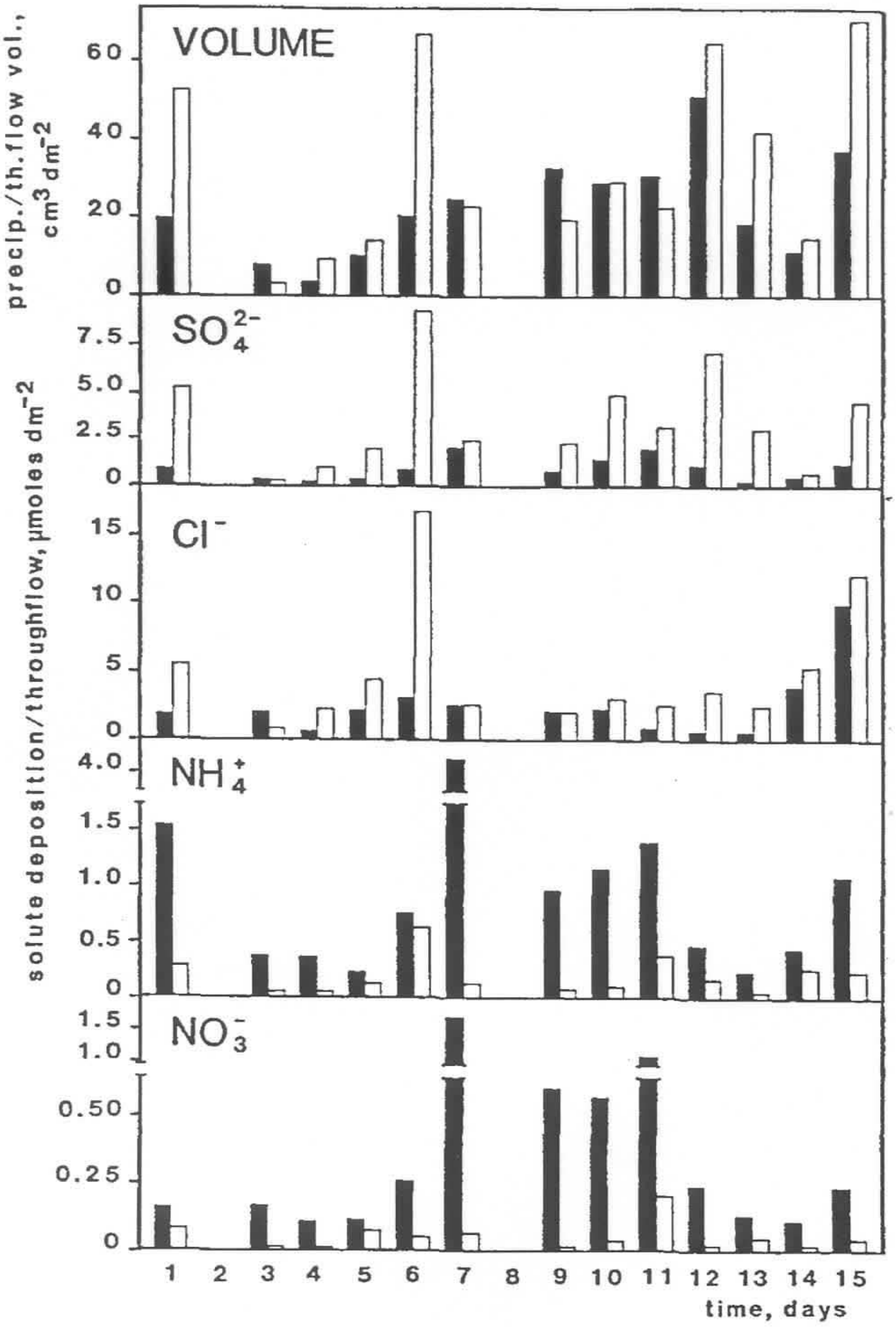

Fig. 6. Cumulative precipitation volume (cm³ dm^{-2}), sulphate, chloride, ammonium and nitrate (µmol dm^{-2}) deposited to (■) and passing through (□) mats of *Sphagnum capillifolium* transplanted from North Wales to the southern Pennines in April 1985. Data from Woodin and Lee (1987a).

a mechanism for restricting further nitrogen assimilation. The loss of nitrate reductase induction following successive rain events by the 'unpolluted' population suggests that under these conditions at least the supply of combined nitrogen at the polluted site can quickly become supra-optimal.

A consequence of the supply of combined nitrogen being supra-optimal for growth of *Sphagnum* is that the deposited nitrogen would no longer be immobilized by the bryophyte carpet. Figure 6 shows the results of a lysimeter experiment in the polluted southern Pennines similar to those described above. *Sphagnum capillifolium* from a North Wales site was used for this experiment. The results show that although much of the nitrate and ammonium supply was immobilized, at every rain event detectable quantities of these ions were present in throughflow. This figure also shows that bulk deposition is a very poor indicator of element supply to a *Sphagnum* carpet. Throughflow volume in lysimeters containing *Sphagnum* was 32% greater overall than bulk deposition collected in adjacent gauges of similar dimensions but lacking the moss. Bulk deposition also did not account for 68% of sulphate throughfall and 47% of chloride. The simplest explanation of the volume discrepancy is that the moss surface is a much more efficient intercepter of occult deposition than the bulk deposition gauge. Bulk collectors are known to be inefficient collectors of occult deposition, and at a site where wind-driven fog and cloud are prevalent, these must markedly underestimate the atmospheric supply. It would appear that occult deposition is an important source of elements for *Sphagnum* at this site, and this accounts at least in part for the increase in chloride and sulphate in throughflow. Woodin and Lee (1987a) also showed that nitrate in occult deposition produced a greater induction of nitrate reductase activity in *Sphagnum* than the same concentration of the ion in large droplet deposition suggesting that bryophytes are particularly adapted to utilize the element supply in mist and cloud. *Sphagnum* may also be an efficient surface for the collection of dry deposition. The comparison of volume collection by the bulk collectors and the *Sphagnum* lysimeters also demonstrates that the nitrogen supply to the moss surface must have been much higher than the bulk deposit would indicate.

The observations at the polluted southern Pennine site revealed detectable quantities of nitrate and ammonium ions in *Sphagnum* throughflow unlike the situation in subarctic mires. However, over the short exposure time (15 dyas), no massive breakdown of the sink for these ions occurred in this species. That this can occur in *Sphagnum capillifolium* was demonstrated by a laboratory experiment (Woodin and Lee 1987a) in which the moss was sprayed daily with high concentrations of nitrate and (0.5 mM nitrate or 0.5 mM nitrate plus 0.75 mM ammonium). Although these concentrations are high, they are well within the range observed in occult deposition. There was a progressive loss of the ability of the moss to immobilize nitrogen; at the end of the experimental period (11 days), 48% of the nitrate applied daily appeared in the throughflow of the nitrate treatment and 86% in the nitrate plus ammonium treatment. Thus it is likely that given sufficient time, a general breakdown of the ability to immobilize the atmospheric combined nitrogen supply would have occurred in the case of *Sphagnum capillifolium* at the polluted site, and Press *et al.* (1986) demonstrated that this was the case for the indigenous *S. cuspidatum*.

Ecological consequences of a breakdown of mire structure

The bryophyte carpet, composed of plants with thin leaves continuously exposed to atmospheric deposition, is the primary recipient of much of the atmospheric pollution loading to ombrotrophic mire surfaces. As a normal part of their adaptation to growth in an environment in which the supply of essential elements is mainly from the atmosphere and may be extremely low, many bryophyte species have the ability to accumulate aerially-derived elements (see *e.g.*, Brown 1982). If the rate of supply is low, *Sphagnum* species may accumulate the pollutant element with little if any effect on growth, and little if any initial penetration of the pollutant into the rooting zones of the higher plants. Thus the structure of the mire ecosystem and the growth of the mire plants may be unaffected. Later, a proportion of the pollutant element supply may become available in the rooting zones as the *Sphagnum* grows and the old stems decay, but this may be only a small proportion of the total deposited and the form in which it becomes available may well differ from the original atmospheric supply.

At a higher pollutant loading, the *Sphagnum* species may not be able to immobilize all the pollutant supply, and the pollutant immediately enters the rooting zones of the higher plants. This may perhaps be achieved with no detectable effect on the growth of the bryophytes, and thus the structure of the mire is apparently unaltered. However the increased supply of elements to higher plants may influence their growth. In the case of nitrogen, this might stimulate higher plant growth and thus their competitive ability which could in due course adversely affect *Sphagnum* growth since one of the mechanisms which may lead to dominance would be lost. The increased solute supply might also reduce the growth of the higher plants. Most higher plants of mires for example are adapted to an ammonium-based nutrition (Marthaler 1939; Ellenberg 1977), and it is possible that nitrate entering the rooting zones of these plants may have some adverse effects on their mineral nutrition and growth. However, it is unlikely that detrimental effects on higher plants would be observed before any effect on bryophyte growth became apparent since bryophytes are generally much more sensitive to increases in solute supply than are higher plants. Thus more probably, as pollutant deposition increases, the growth of *Sphagnum* decreases, and with it the 'sink' of the bryophyte carpet for atmospheric elements.

In the limit, the growth is so severely affected that the bryophyte carpet is removed and only higher plants remain. This process has occurred on many bog surfaces in the southern Pennines of England since the Industrial Revolution as the result of atmospheric pollution (see *e.g.*, Lee *et al.* 1987), the once species-rich mire communities being replaced by impoverished ones in which *Eriophorum* species are dominant. These mires are exceptional in being almost devoid of any bryophyte cover. This complete modification of structure has markedly affected the hydrology of the mires, and also the chemical composition of the drainage waters. Nitrate, close to the limits of detection in unpolluted mire waters, is readily measurable in southern Pennine stream waters draining the bogs,and aluminium is mobilized. The direct input of elements into the peat surface without modification of the living *Sphagnum* carpet must also have affected the microbial communities (see *e.g.*, Press *et al.* 1985), and may have influenced decomposition rates and peat formation. Thus Clymo and Hayward (1982) showed that the decay of mire plants was positively correlated with nitrogen concentration, the very slow decomposition rate of *Sphagnum* species being associated with usually very low tissue nitrogen concentrations. These mires are also very severely eroded in places, a process which may have been accelerated by the loss of bryophyte cover.

To what extent these processes are occurring elsewhere in less grossly polluted mires is uncertain. The general increase in atmospheric nitrogen and sulphur supply in the northern hemisphere during the last two centuries since the beginning of the Industrial Revolution is most likely to be influencing the ecology of many ombrotrophic mires, if only in subtle ways, perhaps affecting the primary element limitation on growth or the relative competitive abilities of *Sphagnum* species. In this regard, perhaps the increased atmospheric element supply is contributing to the present-day success of *Sphagnum recurvum* P. Beauv. in northern Europe (see *e.g.*, Tallis 1973). Ombrotrophic mires are potentially amongst the most sensitive of ecosystems to atmospheric pollution being dominated by bryophytes adapted to growth in low concentrations of solutes and being dependent on an atmospheric supply of elements. Further studies are required to assess the extent to which changes are occurring in the structure of ombrotrophic mires in the northern hemisphere in response to atmospheric pollution. These studies could also prove invaluable in predicting and providing an early warning of pollution-induced changes in less sensitive ecosystems.

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